



Influence of salinity and water content on soil microorganisms

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Abstract

Salinization is one of the most serious land degradation problems facing world. Salinity results in poor plant growth and low soil microbial activity due to osmotic stress and toxic ions. Soil microorganisms play a pivotal role in soils through mineralization of organic matter into plant available nutrients. Therefore it is important to maintain high microbial activity in soils. Salinity tolerant soil microbes counteract osmotic stress by synthesizing osmolytes which allows them to maintain their cell turgor and metabolism. Osmotic potential is a function of the salt concentration in the soil solution and therefore affected by both salinity (measured as electrical conductivity at a certain water content) and soil water content. Soil salinity and water content vary in time and space. Understanding the effect of changes in salinity and water content on soil microorganisms is important for crop production, sustainable land use and rehabilitation of saline soils. In this review, the effects of soil salinity and water content on microbes are discussed to guide future research into management of saline soils. © 2015 International Research and Training Center on Erosion and Sedimentation and China Water and Power Press. Production and Hosting by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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1. Introduction

It is predicted that the human population will reach 8 billion in 2025. To avoid or minimize food shortage, saline soils have to be rehabilitated and managed to meet the food demand of an ever growing human population (Ladeiro, 2012). Soil microorganisms constitute less than 0.5% (w/w) of the soil mass, but they play a key role in soil properties and processes. Salinity affects plants and microbes via two primary mechanisms: osmotic effect and specific ion effects (Oren, 1999; Chhabra, 1996). Another factor influencing plants and microbes is soil water content. Soil water potential which relates to the energy level by which the water is held in the soil also closely related to soil salinity, it is influenced by osmotic potential in the soil solution.

2. The importance of soil microorganisms for nutrient cycling

Soil microorganisms constitute less than 0.5% (w/w) of the soil mass, but they play a key role in soil properties and processes. Soil microbes include bacteria, archaea, fungi, protozoa and viruses (Tate, 2000). Microorganisms participate in oxidation, nitrification, ammonification, nitrogen fixation, and other processes which lead to decomposition of soil organic matter and transformation of nutrients (Amato & Ladd, 1994), they can also store C and nutrients in their biomass which are mineralized after cell death by surviving microbes (Anderson & Domsch, 1980). Our understanding of these processes increased considerably in recent years with advances in molecular and analytical methodologies which have led to more successful strategies to modify them for a range of ecosystem services (Frey, Six, & Elliott, 2003; Gessner et al., 2010; Rillig & Mummey, 2006).

Nutrient cycling is the flux of nutrients within and between the various biotic or abiotic pools in which nutrients occur in the soil environment (Brady & Weil, 2002). Microorganisms have a major impact on the cycling of elements, most of which are essential for the growth of living organisms. Bacteria, archaea and fungi, in particular, are crucial for the cycling of several important inorganic nutrients in soils. Through oxidation, ammonification, nitrogen fixation and other processes, organic materials are decomposed, releasing essential inorganic plant nutrients to the soil. Nitrate (through nitrification), sulfate (through sulfur oxidation), phosphate (through phosphorus mineralization) are present in soils primarily due to the action of microorganisms. Therefore, microbes are essential to maintain a productive and valuable soil system. Disturbance of the soil environment, such as land use change or soil cultivation, can shift microbial communities and can have detrimental effects on soil nutrient cycling (French et al., 2009).

In addition, the emission of CO₂ from soils, which includes respiration from soil organisms and roots, contributes approximately 10% to atmospheric CO₂ (Raich & Potter, 1995). Microbes also play an essential role in the formation of humic substances which are stable forms of organic C and critical for organic C sequestration in soils (Burns et al., 1986). (Fig. 1).

3. Soil salinity

3.1. Soil salinity definition

A soil that contains excess salts so as to impair its productivity is called a salt-affected soil. Salt in the soil can influence soil processes through the salt concentration in the soil solution (salinity) which determines the osmotic potential and the concentration of sodium on the exchange complex of the soil (sodicity) which influences soil structural stability. Salinity can, over time, lead to sodicity. The major soluble salts in soils are the cations Na⁺ (sodium), Ca²⁺ (calcium), Mg²⁺ (magnesium) and K⁺ (potassium), and the anions Cl⁻ (chloride), SO₄²⁻ (sulfate), HCO₃⁻ (bicarbonate), CO₃²⁻ (carbonate) and NO₃⁻ (nitrate) (Shi & Wang, 2005). There are several classification systems for salt-affected soils in the world, for example the USDA system, the USSR system and the Australian

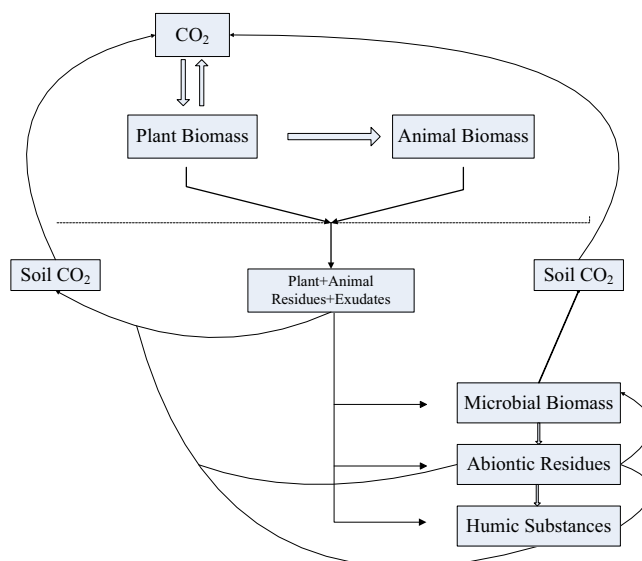


Fig. 1. Conceptual model of carbon cycle emphasizing transfers between major soil organic matter pools (Tate, 2000).

Table 1
Classification of salt-affected soils.

Salt-affected soil classification	EC _e (dS m ⁻¹)	pH	Sodium adsorption ratio	Soil physical condition
Saline	> 4.0	< 8.5	< 13	Normal
Saline–sodic	> 4.0	< 8.5	> 13	Normal
Sodic	< 4.0	> 8.5	> 13	Poor

system (Chhabra, 1996). The USDA system classifies soils in three distinct categories (saline, sodic and saline–sodic soils). Saline soils have an electrical conductivity of the saturated paste (EC_e) > 4 dS m⁻¹, ESP < 15 or SAR < 13 and pH < 8.5. Sodic soils have an ESP > 15 or SAR > 13. Soils that have both detrimental levels of neutral soluble salts (EC_e > 4 dS m⁻¹) and a high-proportion of sodium ions (ESP > 15 or SAR > 13) are classified as saline–sodic soils (Brady & Weil, 2002; CISEAU, IPTRID, AGLL, & FAO, 2005) (Table 1). Salt-affected soils can be classified according to how the salinity developed: primary salinity which occurs naturally where the soil parent material is rich in soluble salts, or geochemical processes result in salt-affected soil. Secondary salinity is salinization of land and water resources due to human activities. Human activities which can induce salinization include poor irrigation management; insufficient drainage; improper cropping patterns and rotations; chemical contamination (Oldeman, Hakkeling, & Sombroek, 1990; UNEP, 2007).

3.2. Effects of salinity on microorganisms

High-concentrations of soluble salts affect microbes via two primary mechanisms: osmotic effect and specific ion effects.

Soluble salts increase the osmotic potential (more negative) of the soil water, drawing water out of cells which may kill microbes and roots through plasmolysis. Low osmotic potential also makes it more difficult for roots and microbes to remove water from the soil (Oren, 1999). Plants and microbes can adapt to low osmotic potential by accumulating osmolytes, however, synthesis of osmolytes requires large amounts of energy and this results in reduced growth and activity (Oren, 1999; Wichern, Wichern, & Joergensen, 2006). At high-concentrations, certain ions, including Na⁺, Cl⁻, and HCO₃⁻, are toxic to many plants (Chhabra, 1996).

Many studies showed that salinity reduces microbial activity, microbial biomass and changes microbial community structure (Andronov et al., 2012; Batra & Manna, 1997; Pathak & Rao, 1998; Rousk, Elyaagubi, Jones, & Godbold, 2011; Setia, Marschner, Baldock, Chittleborough, & Verma, 2011). Salinity reduces microbial biomass mainly because the osmotic stress results in drying and lysis of cells (Batra & Manna, 1997; Laura, 1974; Pathak & Rao, 1998; Rietz & Haynes, 2003; Sarig, Fliessbach, & Steinberger, 1996; Sarig & Steinberger, 1994; Yuan, Li, Liu, Gao, & Zhang, 2007a). Some studies showed that soil respiration decreased with increasing soil EC (Adviento-Borbe, Doran, Drijber, & Dobermann, 2006; Wong, Dalal, & Greene, 2009; Yuan et al., 2007b). Setia, Marschner, Baldock, and Chittleborough (2010) found that soil respiration was reduced by more than 50% at $EC_{1:5} \geq 5.0 \text{ dS m}^{-1}$. However, Rietz and Haynes (2003) reported that soil respiration was not significantly correlated with EC, but as EC increased, the metabolic quotient (respiration per unit biomass) increased. The sensitivity of soil enzyme activities to salinity varies: activities of urease, alkaline phosphatase, β -glucosidase were strongly inhibited by salinity (Frankenberger & Bingham, 1982; Pan, Liu, Zhao, & Wang, 2013), whereas dehydrogenase and catalase were less affected (Garcia & Hernandez, 1996).

As explained above, microorganisms have the ability to adapt to or tolerate stress caused by salinity by accumulating osmolytes (Del Moral, Quesada, & Ramos-Cormenzana, 1987; Quesada, Ventosa, Ramoscormenzana, & Rodriguezvalera, 1982; Sagot et al., 2010; Zahran, Moharram, & Mohammad, 1992). Proline and glycine betaine are the main organic osmolytes and potassium cations are the most common inorganic solutes used as osmolytes accumulated by salinity tolerant microbes (Csonka, 1989). However, the synthesis of organic osmolytes requires high-amounts of energy (Killham, 1994; Oren 2001). Accumulation of inorganic salts as osmolytes can be toxic therefore it is confined to halophytic microbes which evolved salt tolerant enzymes to survive in highly saline environments. Fungi tend to be more sensitive to salt stress than bacteria (Gros, Poly, Monrozier, & Faivre, 2003; Pankhurst, Yu, Hawke, & Harch, 2001; Sardinha, Muller, Schmeisky, & Joergensen, 2003; Wichern et al., 2006), thus the bacteria/fungi ratio can be increased in saline soils. Differences in salinity tolerance among microbes results in changes in community structure compared to non-saline soils (Gros et al., 2003; Pankhurst et al., 2001).

4. The effects of soil water availability on microorganisms

4.1. Forms of water in soils

Substantial volumes of water are commonly stored in soils. For example, 1ha of medium textured soil (1 m deep) with a water content at field capacity of 20% can store $8.0 \times 10^5 \text{ L}$ water (Or & Wraith, 2000). Plants and organisms rely heavily on water in soils and water is essential for nutrient cycling. However, soil water content varies both in time and in space which not only influences water availability to plants and microbes but also has a major effect on the rate of diffusion of solutes and gases (Adl, 2003).

The status of soil water can be described in two ways: the soil water content, which indicates how much water is present, and soil water potential, which relates to the energy level by which the water is held in the soil. The water potential is the amount of pressure that needs to be applied to transport a solution of known molarity from a referenced elevation to that of pure water (McKenzie, 2002), mainly including matric, osmotic and gravitational potential. Processes dealing with water balance are usually more related to water content; whereas processes related to water movement are mainly related to soil water potential (Warrick & Or, 2007).

4.2. Effect of water content on microbes

Water is not only an essential transport medium for substrates, it is also an important participant in hydrolysis processes. Therefore soil water content controls microbial activity and is a major factor that determines the rates of mineralization (Paul et al., 2003). However, excess soil water content results in limited O_2 diffusion because O_2 diffusion in water is much lower (about 10^4 times) than in air which will reduce the activity of aerobic microorganisms (Kozłowski, 1984; Skopp, Jawson, & Doran, 1990), but could increase the activities of anaerobes. Lack of water reduces microbial activity and growth (Bottner, 1985; Kieft, Soroaker, & Firestone, 1987), C and N mineralization (Pulleman & Tietema, 1999; Sleutel et al., 2008) and shifts microbial community structure (Hueso, Garcia, & Hernandez, 2012; Sorensen, Germino, & Feris, 2013). Cells retain sufficient water for cell turgor and metabolism by maintaining a higher osmotic potential (more negative) in the cytoplasm than that of the surrounding

environment (Martin, Ciulla, & Roberts, 1999). At low water content (high water potential), soil microbes can accumulate organic and inorganic compounds which increases the osmotic potential inside their cells. Therefore the principal tolerance mechanism for low water content and high-salinity is the same: accumulation of osmolytes. Further as soils dry out, substrate supply becomes increasingly limited because the pores drain and water films around aggregates become thinner and disconnected (Ilstedt, Nordgren, & Malmer, 2000; Stark & Firestone, 1995).

Fungi, Gram-positive bacteria and archaea can better tolerate high matric potential than Gram-negative bacteria because they have stronger cell walls (Fierer, Schimel, & Holden, 2003; Martin et al., 1999; Schimel, Balser, & Wallenstein, 2007; Vasileiadis et al., 2012).

4.3. Effect of fluctuating water content on soil microorganisms

Soil moisture and the distribution of water within a soil profile vary with seasonal cycles of rainfall, irrigation periods (farm lands) and temperature. In semi-arid and Mediterranean ecosystems, surface soils frequently experience long dry periods followed by a relatively rapid wetting (Fierer & Schimel, 2002). The effects of drying and rewetting on soil microbial processes have been studied (Griffiths, Whiteley, O'Donnell, & Bailey, 2003; Herron, Stark, Holt, Hooker, & Cardon, 2009; Ilstedt et al., 2000; Schimel et al., 2007; Xiang, Doyle, Holden, & Schimel, 2008). The concentration of available substrate and microbial activity peak in the first 24 h after rewetting (Fierer & Schimel, 2003). This is because, upon rewetting, cells of sensitive microbes lyse, whilst other microbial genotypes release the organic solutes they accumulated during the dry phase (Halverson, Jones, & Firestone, 2000). Furthermore, soil aggregates break down and their previously protected organic matter is exposed and can then be decomposed. Microbial biomass, activity and nitrification decrease with increasing number of dry and rewetting cycles (Mikha, Rice, & Milliken, 2005; Nelson, Ladd, & Oades, 1996; Wu & Brookes, 2005). The decrease in microbial biomass with increasing number of drying and rewetting cycles may be due to the higher microbial biomass turnover (Van Gestel, Merckx, & Vlassak, 1993) and the loss of C during the flush in respiration upon rewetting (Fierer & Schimel, 2003). However, the response of microbial activity to drying and rewetting varies with soil type (Jin, Haney, Fay, & Polley, 2013) which may be due to the interaction of soil moisture and soil type, aggregation and the concentration of potentially bioavailable soil organic matter (Anderson & Ingram, 1993). However, drying and rewetting can also kill some microbes and change microbial community structure which, in turn, could influence nutrient cycling (Fierer et al., 2003; Schimel et al., 2007). Butterly, Bunemann, McNeill, Baldock, and Marschner (2009) found that drying and rewetting induced a reduction in fungi and an increase in Gram-positive bacteria (Butterly et al., 2009).

5. Conclusion

Soil salinity is a threat world-wide to agricultural production and ecosystems because it reduces plant growth and microbial functioning. The effects of salinity and soil water content on soil microbes have been studied extensively, but usually separately, in saline soils, the water content also influences the salt concentration in the soil solution (osmotic potential), the study of interaction between soil water content and salinity on soil microbes is needed. Further in the field, soil salinity and water content are not constant in time and space. Therefore, experiments are needed to better understand the effect of fluctuating salinity and soil water content on soil microbes. Synthesis of osmolytes requires large amounts of energy. Therefore addition of organic materials such as plant residues or manures as nutrient sources for microbes may be an important strategy to ameliorate saline soils. Future research could investigate the effect the properties of organic materials such as decomposability and nutrient content on microbial tolerance to osmotic stress.

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References

Adl, S. M. (2003). *The ecology of soil decomposition*. Wallingford UK: CAB International 2003.

- Adviento-Borbe, M. A.A., Doran, J. W., Drijber, R. A., & Dobermann, A. (2006). Soil electrical conductivity and water content affect nitrous oxide and carbon dioxide emissions in intensively managed soils. *Journal of Environmental Quality*, 35, 1999–2010.
- Amato, M., & Ladd, J. N. (1994). Application of the ninhydrin-reactive N assay for microbial biomass in acid soils. *Soilless Biology Biochemistry*, 26, 1109–1115.
- Anderson, J. M., & Ingram, J. S.I. (1993). *Tropical soil biology and fertility. A handbook of methods* ((Second edition). Wallingford, England: CAB International.
- Anderson, J. P.E., & Domsch, K. H. (1980). Quantities of plant nutrients in the microbial biomass of selected soils. *Soilless Science*, 130, 211–216.
- Andronov, E. E., Petrova, S. N., Pinaev, A. G., Pershina, E. V., Rakhimgalieva, S. Z., Akhmedenov, K. M., ... Sergaliev, N. K. (2012). Analysis of the structure of microbial community in soils with different degrees of salinization using T-RFLP and real-time PCR techniques. *Eurasian Soilless Science*, 45, 147–156.
- Batra, L., & Manna, M. C. (1997). Dehydrogenase activity and microbial biomass carbon in salt affected soils of semiarid and arid regions. *Arid Land Research and Management*, 11, 295–303.
- Bottner, P. (1985). Response of microbial biomass to alternate moist and dry conditions in a soil incubated with C-14 labeled and N-15 labelled plant material. *Soilless Biology Biochemistry*, 17, 329–337.
- Brady, N. C., & Weil, R. R. (2002). *The nature and properties of soils*. New Jersey: Prentice Hall.
- Burns, R. G., Dell'Agnola, G., Miele, S., Nardi, G., Savoini, M., Schnitzer, ... Visser, S. A. (1986). *Humic substances effect on soil and plants*. Ramo Editoriale degli Agricoltori.
- Butterly, C. R., Bunemann, E. K., McNeill, A. M., Baldock, J. A., & Marschner, P. (2009). Carbon pulses but not phosphorus pulses are related to decreases in microbial biomass during repeated drying and rewetting of soils. *Soilless Biology Biochemistry*, 41, 1406–1416.
- Chhabra, R. (1996). *Soil salinity and water quality*. Rotterdam, The Netherlands: Balkema.
- CISEAU, IPTRID, AGLL, FAO. (2005). *Management of irrigation-induced salt-affected soils*.
- Csonka, L. N. (1989). Physiological and genetic responses of bacteria to osmotic stress. *Microbiological Reviews*, 53, 121–147.
- Del Moral, A., Quesada, E., & Ramos-Cormenzana, A. (1987). Distribution and types of bacterial isolated from an inland saltern Annales de l'Institut Pasteur. *Microbiology*, 138, 59–66.
- Fierer, N., & Schimel, J. P. (2002). Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soilless Biology Biochemistry*, 34, 777–787.
- Fierer, N., & Schimel, J. P. (2003). A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soilless Science Society of America Journal*, 67, 798–805.
- Fierer, N., Schimel, J. P., & Holden, P. A. (2003). Influence of drying–rewetting frequency on soil bacterial community structure. *Microbial Ecology*, 45, 63–71.
- Frankenberger, W. T., & Bingham, F. T. (1982). Influence of salinity on soilless enzyme activities. *Soilless Science Society of America Journal*, 46, 1173–1177.
- French, S., Levy-Booth, D., Samarajeewa, A., Shannon, K. E., Smith, J., & Trevors, J. T. (2009). Elevated temperatures and carbon dioxide concentrations: effects on selected microbial activities in temperate agricultural soils. *World Journal of Microbiology Biotechnology*, 25, 1887–1900.
- Frey, S. D., Six, J., & Elliott, E. T. (2003). Reciprocal transfer of carbon and nitrogen by decomposer fungi at the soil–litter interface. *Soilless Biology Biochemistry*, 35, 1001–1004.
- Garcia, C., & Hernandez, T. (1996). Influence of salinity on the biological and biochemical activity of a calciorthird soil. *Plant and Soilless*, 178, 255–263.
- Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hattenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology Evolution*, 25, 372–380.
- Griffiths, R. I., Whiteley, A. S., O'Donnell, A. G., & Bailey, M. J. (2003). Physiological and community responses of established grassland bacterial populations to water stress. *Applied and Environmental Microbiology*, 69, 6961–6968.
- Gros, R., Poly, F., Monrozier, L. J., & Faivre, P. (2003). Plant and soil microbial community responses to solid waste leachates diffusion on grassland. *Plant and Soilless*, 255, 445–455.
- Halverson, L. J., Jones, T. M., & Firestone, M. K. (2000). Release of intracellular solutes by four soil bacteria exposed to dilution stress. *Soilless Science Society of America Journal*, 64, 1630–1637.
- Herron, P. M., Stark, J. M., Holt, C., Hooker, T., & Cardon, Z. G. (2009). Microbial growth efficiencies across a soil moisture gradient assessed using ¹³C-acetic acid vapor and ¹⁵N-ammonia gas. *Soilless Biology Biochemistry*, 41, 1262–1269.
- Hueso, S., Garcia, C., & Hernandez, T. (2012). Severe drought conditions modify the microbial community structure, size and activity in amended and unamended soils. *Soilless Biology Biochemistry*, 50, 167–173.
- Ilstedt, U., Nordgren, A., & Malmer, A. (2000). Optimum soil water for soil respiration before and after amendment with glucose in humid tropical acrisols and a boreal mor layer. *Soilless Biology Biochemistry*, 32, 1591–1599.
- Jin, V. L., Haney, R. L., Fay, P. A., & Polley, H. W. (2013). Soil type and moisture regime control microbial C and N mineralization in grassland soils more than atmospheric CO₂-induced changes in litter quality. *Soilless Biology Biochemistry*, 58, 172–180.
- Kieft, T. L., Sorokey, E., & Firestone, M. K. (1987). Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soilless Biology Biochemistry*, 19, 119–126.
- Killham, K. (1994). *Soil ecology* (pp. 152–154) UK: Cambridge University Press 152–154.
- Kozlowski, T. T. (1984). *Flooding and plant growth*. Orlando, Fla: Academic Press.
- Ladeiro, B. (2012). Saline agriculture in the 21st century: using salt contaminated resources to cope food requirements. *Journal of Botany*, 2012, 7.
- Laura, R. D. (1974). Effects of neutral salts on carbon and nitrogen mineralization of organic-matter in soil. *Plant and Soilless*, 41, 113–127.
- Martin, D. D., Ciulla, R. A., & Roberts, M. F. (1999). Osmoadaptation in archaea. *Applied and Environmental Microbiology*, 65, 1815–1825.

- McKenzie, N. (2002). *Soil physical measurement and interpretation for land evaluation*. Melbourne: CSIRO PUBLISHING. [electronic resource].
- Mikha, M. M., Rice, C. W., & Milliken, G. A. (2005). Carbon and nitrogen mineralization as affected by drying and wetting cycles. *Soilless Biology Biochemistry*, 37, 339–347.
- Nelson, P. N., Ladd, J. N., & Oades, J. M. (1996). Decomposition of C-14-labelled plant material in a salt-affected soil. *Soilless Biology Biochemistry*, 28, 433–441.
- Oldeman, L. R., Hakkeling, R. T. A., Sombroek, W. G. (1990). *World map of the status of human-induced soil degradation: an explanatory note*.
- Or, D., & Wraith, J. M. (2000). Soil water content and water potential relationships. In: M. E. Sumner. (Ed.), *Handbook of soil science* (pp. A53–A65). Boca Raton: CRC Press.
- Oren, A. (1999). Bioenergetic aspects of halophilism. *Microbiology and Molecular Biology Reviews*, 63, 334–340.
- Oren, A. (2001). The bioenergetic basis for the decrease in metabolic diversity at increasing salt concentrations: implications for the functioning of salt lake ecosystems. *Hydrobiologia*, 466, 61–72.
- Pan, C. C., Liu, C. A., Zhao, H. L., & Wang, Y. (2013). Changes of soil physico-chemical properties and enzyme activities in relation to grassland salinization. *European Journal of Soilless Biology*, 55, 13–19.
- Pankhurst, C. E., Yu, S., Hawke, B. G., & Harch, B. D. (2001). Capacity of fatty acid profiles and substrate utilization patterns to describe differences in soil microbial communities associated with increased salinity or alkalinity at three locations in South Australia. *Biology and Fertility of Soils*, 33, 204–217.
- Pathak, H., & Rao, D. L.N. (1998). Carbon and nitrogen mineralization from added organic matter in saline and alkali soils. *Soilless Biology Biochemistry*, 30, 695–702.
- Paul, K. I., Polglase, P. J., O'Connell, A. M., Carlyle, J. C., Smethurst, P. J., & Khanna, P. K. (2003). Defining the relation between soil water content and net nitrogen mineralization. *European Journal of Soilless Science*, 54, 39–47.
- Pulleman, M., & Tietema, A. (1999). Microbial C and N transformations during drying and rewetting of coniferous forest floor material. *Soilless Biology Biochemistry*, 31, 275–285.
- Quesada, E., Ventosa, A., Ramoscormenzana, A., & Rodriguezvalera, F. (1982). Types and properties of some bacteria isolated from hypersaline soils. *Journal of Applied Bacteriology*, 53, 155–161.
- Raich, J. W., & Potter, C. S. (1995). Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles*, 9, 23–36.
- Rietz, D. N., & Haynes, R. J. (2003). Effects of irrigation-induced salinity and sodicity on soil microbial activity. *Soilless Biology Biochemistry*, 35, 845–854.
- Rillig, M. C., & Mummey, D. L. (2006). Mycorrhizas and soil structure. *Newly Phytologist*, 171, 41–53.
- Rousk, J., Elyaagubi, F. K., Jones, D. L., & Godbold, D. L. (2011). Bacterial salt tolerance is unrelated to soil salinity across an arid agroecosystem salinity gradient. *Soilless Biology Biochemistry*, 43, 1881–1887.
- Sagot, B., Gaysinski, M., Mehiri, M., Guignon, J. M., Le Rudulier, D., & Alloing, G. (2010). Osmotically induced synthesis of the dipeptide N-acetylglutaminylglutamine amide is mediated by a new pathway conserved among bacteria. *Proceedings of the National Academy of Sciences*, 107, 12652–12657.
- Sardinha, M., Muller, T., Schmeisky, H., & Joergensen, R. G. (2003). Microbial performance in soils along a salinity gradient under acidic conditions. *Applied Soilless Ecology*, 23, 237–244.
- Sarig, S., Fliessbach, A., & Steinberger, Y. (1996). Microbial biomass reflects a nitrogen and phosphorous economy of halophytes grown in salty desert soil. *Biology and Fertility of Soils*, 21, 128–130.
- Sarig, S., & Steinberger, Y. (1994). Microbial biomass response to seasonal fluctuation in soil-salinity under the canopy of desert halophytes. *Soilless Biology Biochemistry*, 26, 1405–1408.
- Schimel, J., Balser, T. C., & Wallenstein, M. (2007). Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, 88, 1386–1394.
- Setia, R., Marschner, P., Baldock, J., & Chittleborough, D. (2010). Is CO₂ evolution in saline soils affected by an osmotic effect and calcium carbonate?. *Biology and Fertility of Soils*, 46, 781–792.
- Setia, R., Marschner, P., Baldock, J., Chittleborough, D., & Verma, V. (2011). Relationships between carbon dioxide emission and soil properties in salt-affected landscapes. *Soilless Biology Biochemistry*, 43, 667–674.
- Shi, D. C., & Wang, D. L. (2005). Effects of various salt-alkaline mixed stresses on *Aneurolepidium chinense* (Trin.) Kitag. *Plant and Soilless*, 271, 15–26.
- Skopp, J., Jawson, M. D., & Doran, J. W. (1990). Steady-state aerobic microbial activity as a function of soil-water content. *Soilless Science Society of America Journal*, 54, 1619–1625.
- Sleutel, S., Moeskops, B., Huybrechts, W., Vandenbossche, A., Salomez, J., De Bolle, S., ... De Neve, S. (2008). Modeling soil moisture effects on net nitrogen mineralization in loamy wetland soils. *Wetlands*, 28, 724–734.
- Sorensen, P. O., Germino, M. J., & Feris, K. P. (2013). Microbial community responses to 17 years of altered precipitation are seasonally dependent and coupled to co-varying effects of water content on vegetation and soil C. *Soilless Biology Biochemistry*, 64, 155–163.
- Stark, J. M., & Firestone, M. K. (1995). Mechanisms for soil-moisture effects on activity of nitrifying bacteria. *Applied and Environmental Microbiology*, 61, 218–221.
- Tate, R. L. (2000). *Soil microbiology*. New York: John Wiley&Sons.
- UNEP. (2007). *Global Environment Outlook 4*. Malta.
- Van Gestel, M., Merckx, R., & Vlassak, K. (1993). Microbial biomass responses to soil drying and rewetting-the fate of fast-growing and slow-growing microorganisms in soils from different climates. *Soilless Biology Biochemistry*, 25, 109–123.
- Vasileiadis, S., Coppolecchia, D., Puglisi, E., Balloi, A., Mapelli, F., Hamon, R. E., ... Trevisan, M. (2012). Response of ammonia oxidizing bacteria and archaea to acute zinc stress and different moisture regimes in soil. *Microbial Ecology*, 64, 1028–1037.

- Warrick, A. W., & Or, D. (2007). Soil water concepts. In: F. R. Lamm, J. E. Ayars, & F. S. Nakayama (Eds.), *Microirrigation for crop production: design, operation, and management* (pp. 27–30). Oxford: Elsevier B.V.
- Wichern, J., Wichern, F., & Joergensen, R. G. (2006). Impact of salinity on soil microbial communities and the decomposition of maize in acidic soils. *Geoderma*, 137, 100–108.
- Wong, V. N.L., Dalal, R. C., & Greene, R. S.B. (2009). Carbon dynamics of sodic and saline soils following gypsum and organic material additions: a laboratory incubation. *Applied Soilless Ecology*, 41, 29–40.
- Wu, J., & Brookes, P. C. (2005). The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. *Soilless Biology Biochemistry*, 37, 507–515.
- Xiang, S. R., Doyle, A., Holden, P. A., & Schimel, J. P. (2008). Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. *Soilless Biology Biochemistry*, 40, 2281–2289.
- Yuan, B. C., Li, Z. Z., Liu, H., Gao, M., & Zhang, Y. Y. (2007a). Microbial biomass and activity in salt affected soils under arid conditions. *Applied Soilless Ecology*, 35, 319–328.
- Yuan, B. C., Xu, X. G., Li, Z. Z., Gao, T. P., Gao, M., Fan, X. W., & Deng, H. M. (2007b). Microbial biomass and activity in alkalized magnesic soils under arid conditions. *Soilless Biology Biochemistry*, 39, 3004–3013.
- Zahran, H. H., Moharram, A. M., & Mohammad, H. A. (1992). Some ecological and physiological-studies on bacteria isolated from salt-affected soils of Egypt. *Journal of Basic Microbiology*, 32, 405–413.